



Discinoids (Brachiopoda: Lingulata) from the upper Manacapuru Formation (Early Devonian), south border of Amazonas Basin, Brazil

Luiz Felipe Aquino Corrêa^{a,*}, Maria Inês Feijó Ramos^b

^a Universidade Federal do Pará, Rua Augusto Corrêa, 1, Guamá, 66075-110, Belém, PA, Brazil

^b Museu Paraense Emílio Goeldi, Coordenação de Ciências da Terra, Av. Perimetral, 1901, Terra Firme, 66077-830, Belém, PA, Brazil

ARTICLE INFO

Keywords:

Orbiculoidea
Lochkovian
Amazonas basin
Gondwana

ABSTRACT

The taxonomic study of brachiopods (Family Discinidae) from the upper part of the Manacapuru Formation (Lochkovian), south border of the Amazonas Basin, Brazil, allowed to recognize five species of *Orbiculoidea*: *O. bairi*, *O. bodenbenderi*, *O. excentrica*, and two new species described herein: *O. xinguensis* sp. nov. and *O. katzeri* sp. nov. Besides, *O. bairi*, *O. bodenbenderi*, and *O. excentrica* are recorded for the first time in the Manacapuru Formation, and in Northern Brazil, being the oldest records (Lochkovian) of these species in South America too. Their presence in the region can be explained by two reasons: the proximity of the Amazonas Basin, located in northwest Gondwana, during the Early Devonian to the continent of Laurasia (where are recorded most occurrences of *Orbiculoidea* during the Silurian), favoring the specific interchange between these two geographic regions; and the global sea level rise during this time, which flooded a large part of northwestern Gondwana, resulting in the presence of shallow seas in the Amazonas Basin, represented by marine sediments in the upper part of the Manacapuru Formation. These conditions promoted the colonization of inarticulate brachiopods during the Early Devonian in the north of Brazil. The discinoids identified in the strata of the Manacapuru Formation are typical of shallow marine environments, supporting previous interpretations for the upper part of this unit.

1. Introduction

Discinoids are inarticulate brachiopods with organophosphate valves, predominantly marine, that emerged in the Cambrian. Presently, they include four genera, whose distribution is mainly controlled by environmental factors (Emig, 1997; Holmer and Popov, 2000; Zhang et al., 2018). They are important tools for Paleozoic paleobiogeographic studies, which increased in the 21st century (Popov et al., 2013; Winrow and Sutton, 2014; Zhang et al., 2018; Zabini et al., 2019).

Its occurrence in the Ordovician is rare, restricted to low latitudes (Zhang et al., 2018). The Ordovician was marked by global climate changes and the geographical configurations of continental masses, contributing to the Hirnantian Glaciation (Late Ordovician – Early Silurian) that persisted for almost 35 million years (Finnegan et al., 2011). During this time, climatic conditions were quite severe in Gondwana, recording the persistence of only a few discinoids, such as *Kosoidea australis* from the Iapó and Vila Maria formations, Parana Basin (Zabini et al., 2019). During the transition from the Silurian to the Devonian, the melting of the polar ice caps that covered part of Africa

and South America resulted in the maximum marine transgressions covering a large part of the supercontinent Gondwana, mainly the northwest portion (Bolivia, Brazil, Falkland Islands, South Africa, and Australia) (Ludwig, 1964; Carozzi et al., 1973; Caputo, 1984; Caputo and Crowell, 1985; Grahn and Caputo, 1992; Cunha et al., 1994). Such conditions were fundamental for a significant paleogeographic distribution of the brachiopods during the Devonian.

Despite this radiation, the reports of this group are scarce in South America, mainly in the Amazonas and Parnaíba basins. Previous occurrences have been mentioned, although only at a high taxonomic level, such as the records from strata of the Manacapuru (Pridoli-Lochkovian of the Amazonas Basin), Ererê (Eifelian-Givetian of the Amazonas Basin) and Pimenteiras formations (Eifelian-Frasnian of the Parnaíba Basin) (Grahn and Melo, 1990; Wanderley Filho et al., 2005; Fonseca and Ponciano, 2011; Ponciano et al., 2012).

By contrast, in the Parana Basin the discinoids are well known, mainly in the Devonian marine deposits of Ponta Grossa and São Domingos formations, where five species were recorded: *Orbiculoidea bairi* Sharpe (1856); *O. bodenbenderi* Clarke (1913); *O. excentrica* Lange

* Corresponding author.

E-mail addresses: luizfelipe812@gmail.com (L.F.A. Corrêa), mramos@museu-goeldi.br (M.I.F. Ramos).

<https://doi.org/10.1016/j.jsames.2020.102960>

Received 23 June 2020; Received in revised form 12 October 2020; Accepted 12 October 2020

Available online 20 October 2020

0895-9811/© 2020 Elsevier Ltd. All rights reserved.

(1943); *Gigadiscina collis* Clarke (1913), and *Rugadiscina stagona* Commiskey and Bosetti (2017) (Clarke, 1913; Lange, 1943; Zabini et al., 2013; Commiskey et al., 2016; Commiskey and Bosetti, 2017). The absence of taxonomic research on discinoids in the Amazonas and Paranaíba basins hinder the evolutionary understanding of these organisms during the Devonian in Brazil.

This work aims to study the taxonomy of the brachiopods of the family Discinidae found in strata of the Manacapuru Formation (municipality of Vitoria do Xingu), southern border of the Amazonas Basin, contributing to the evolutionary context of this group and enabling correlations at global level.

2. Material and methods

The studied material consists of 272 brachiopod specimens, collected by the TERRAGRAPH PALEONTOLOGIA team between July 2011 and October 2015, in the frame of the project entitled “Paleontological Heritage Rescue Program” of the Belo Monte Hydroelectric Plant, municipality of Vitoria do Xingu, State of Para. Four sampling sites were analyzed: C3P1 (9653975 m N, 413823 m L, zone 22M, SAD 69), C9P1 (9655000 m N, 413261 m L, zone 22M, SAD 69), C13P1 (9653898 m N, 414191 m L, zone 22M, SAD 69), and C14P1 (9648213 m N, 406654 m L, zone 22M, SAD 69) (Fig. 1).

The samples were collected according to the standard methods in paleontology, described in Tomassi et al. (2015a), and referred to the stratigraphic columns. For each specimen an individual number was assigned, with the following pattern: CmPn-X.Y, where Cm corresponds to the collection campaign (C1, C2, C3, ...), Pn is the geographical point within the campaign (P1, P2, P3, ...), X indicates the position in the stratigraphic column, Y is the sequential number of the sample (1,2,3, ...). Figured specimens are housed in the paleontological collection at Museum Paraense Emilio Goeldi, Belem, Para, under catalogue numbers MPEG-3655 to MPEG-3927.

Photographs were taken with a high-resolution digital camera (Canon Powershot A640) attached to an electronic magnifying glass

(LEICA M205 A) and the image capture system. Three valves were extracted from the rock samples (MPEG-3726, MPEG-3728, and MPEG-3746) for being photographed in the scanning electron microscope (SEM) of the research campus of the Museu Paraense Emilio Goeldi. The measures of length (L) and width (W) were obtained with a micrometric lattice of the magnifying glass (LEICA S8AP0).

The taxonomic classification follows Holmer and Popov (2000) for families and genera. Regarding species, the main pertinent articles were consulted: Sharpe (1856), Clarke (1913), Lange (1943), Commiskey and Bosetti (2017), and Carbonaro et al. (2018).

3. Geological setting

The Amazonas Basin is limited to the east by the Gurupa Arch, from the Marajo Basin, and to the west by the Purus Arch from the Solimões Basin (Cunha et al., 2007). It is located in the South American platform, covering an area of about 500.000 km² in the States of Amapa, Amazonas, and Para, north of Brazil (Cunha et al., 1994). This basin is classified as an intracratonic “Type I - Simple Interior” (Klemme, 1980). Its origin has been associated with the dispersion of North-South direction efforts, referring to the closing of the Brazilian cycle (Cunha et al., 2007). After the distensive processes, the magmatic bodies cooled down, initiating the regional thermal subsidence and the emergence of an intracontinental syneclysis. This process formed a basin with elongated geometry, predominantly filled by siliciclastic rocks, essentially Paleozoic, intruded by Mesozoic dikes and diabase sills (Almeida, 1967; Caputo, 1984; Cunha et al., 2007).

According to Cunha et al. (2007), the current stratigraphic framework of the basin presents two first-order mega sequences, one Paleozoic and another Meso-Cenozoic. The Paleozoic mega-sequence is divided into four second-order sequences: Ordovician-Devonian, Devonian-Lower Mississippian, Middle Mississippian, and Pennsylvanian-Permian (Cunha et al., 2007). The Ordovician-Devonian sequence is represented by the Trombetas Group, recording the initial deposition phase in the intracontinental syneclysis of the Amazonas

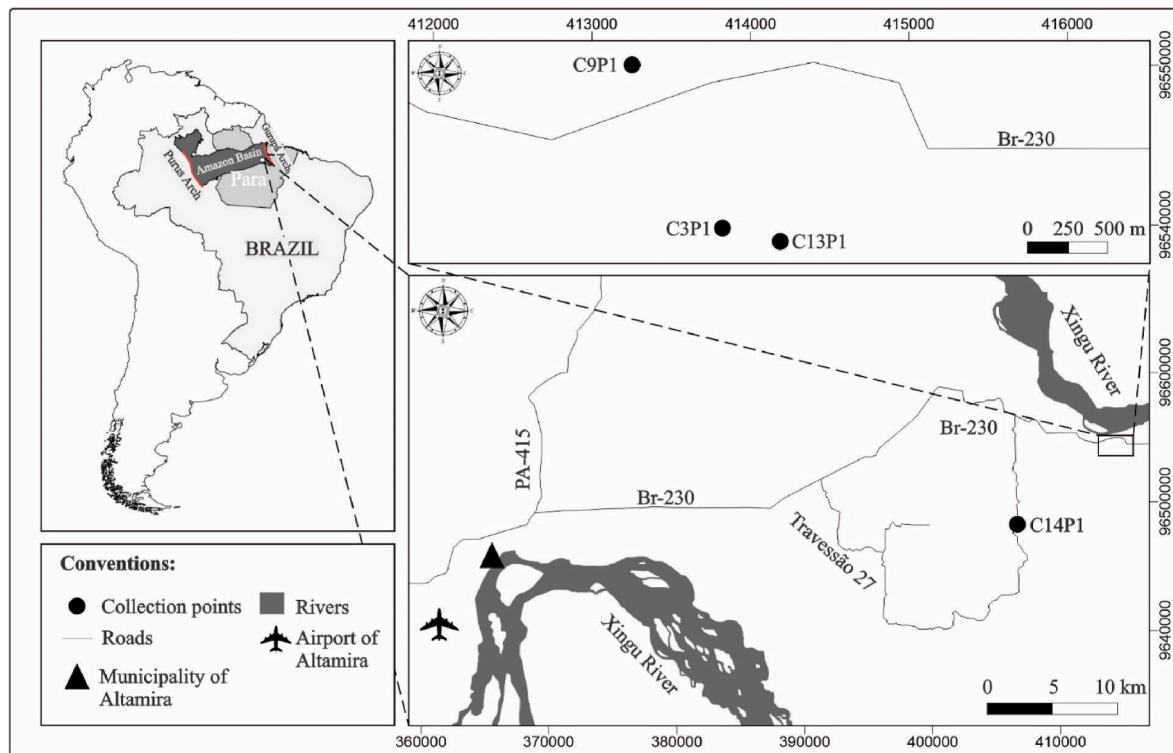


Fig. 1. Location of the study area.
Source: author.

Basin with characteristics of transgressive-regressive cycles (Ludwig 1964; Cunha et al., 1994). Overlaying the Arch of Purus, in the westernmost region of the basin, the strata reflect alternation of glacial and marine environments. In the eastern portion, sedimentation surpassed the Arch Gurupá, favoring the connection with northwest Africa (Cunha et al., 2007). The Trombetas Group (Ludwig, 1964) was considered to be composed of the Autás-Mirim, Nhamundá, Pitinga, and Manacapuru formations (Cunha et al., 1994). Later, Cunha et al. (2007) proposed a new formation in the Trombetas Group, the Jatapu Formation, formerly the Jatapu Member of the Maecuru Formation (Urupadi Group).

The Manacapuru Formation (Caputo, 1984) was first proposed as a member representing the upper part of the old “Trombetas Formation” (Caputo et al., 1971). It is characterized by fine to medium sandstones, neritic and coastal pelites, shales, and laminated siltstones, composing a transgressive-regressive sequence deposited in a deltaic system and shallow platforms (Carozzi et al., 1973; Caputo, 1984; Cunha et al., 1994, 2007; Souza and Nogueira, 2009; Rocha et al., 2019). Biostratigraphic analyses performed by Grahn (2005) established a Pridoli – Lochkovian age for this unit. The fossiliferous content of the

Manacapuru Formation includes brachiopods, conularids, fragments of eurypterids, ichnofossils, palynomorphs, and fishes (Lange, 1967; Quadros, 1985; Janvier and Melo, 1988; Grahn and Melo, 1990; Grahn and Paris, 1992; Granh, 2005; Wanderley Filho et al., 2005; Steemans et al., 2008; Rocha et al., 2019).

4. Results

Of the 272 brachiopods studied samples, 205 are discinoids, 57 are rhynchonelliforms, and 10 are lingulids. The focus of this research is the study of the linguliforms from the Manacapuru Formation belonging to the family Discinidae.

The four sampling sites (C3P1, C9P1, C13P1, and C14P1) were combined in a composite section (Fig. 2), formed from base to top by a crystalline basement, followed by a 0.5 m thick layer of fine-grained massive sandstone with discinoids, interspersed with clay lenses. Above, fine-grained sandstone with incipient lamination and discinoids arranged in almost the entire layer, followed by a laminated siltstone package about 2.1 m in thickness, with discinoids concentrated at its

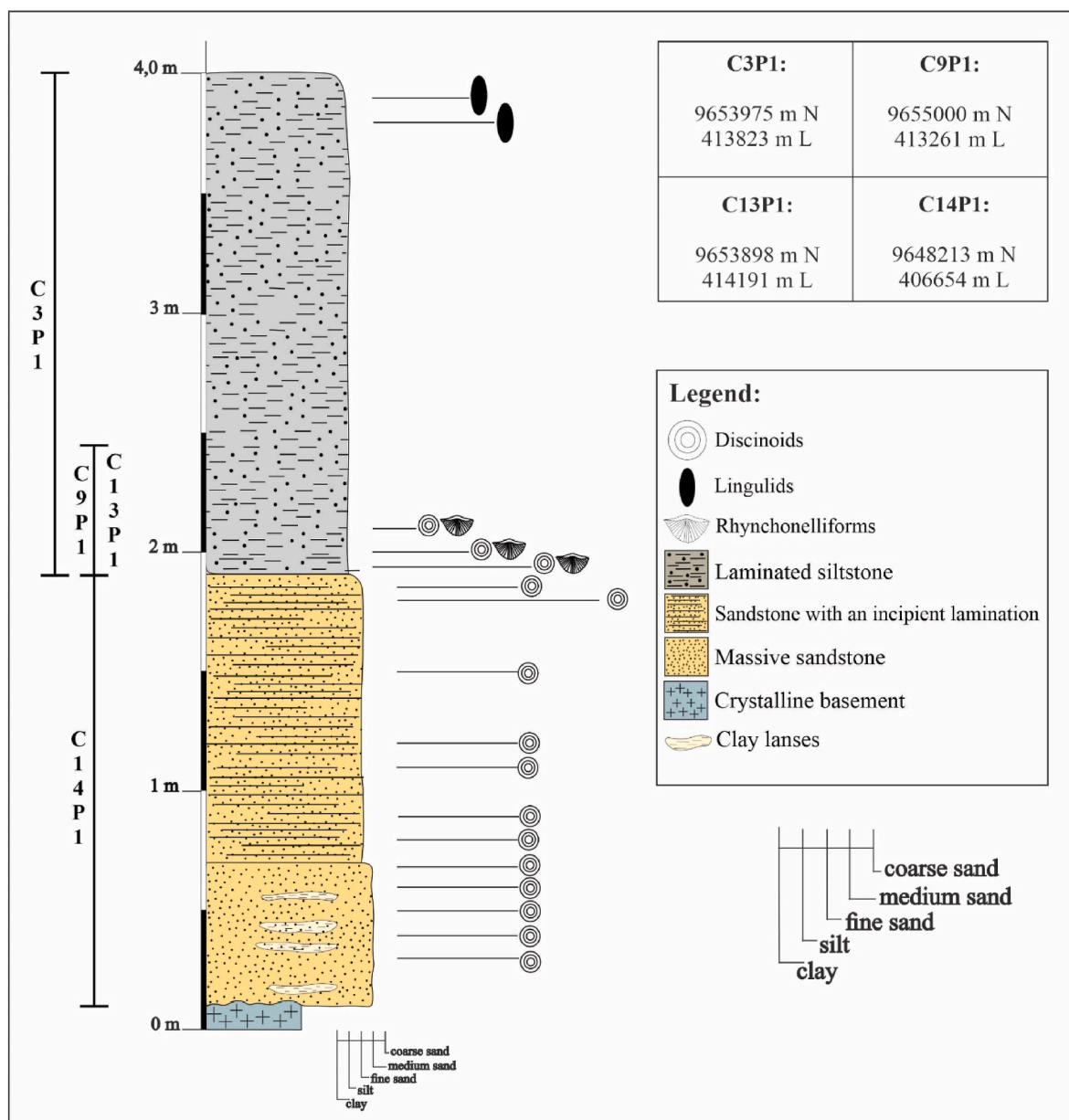


Fig. 2. Composed stratigraphic section of the analyzed sample site. Source: author.

base, always associated with rhynchonelliforms; on the top of the layer, only lingulids occur.

The lithological characteristics of the studied sequence shows that the discinoids occur predominantly in the shallower marine layers, represented by the sandstones of the base, characteristic of shoreface deposits. In addition, they also occur in more fine sediments in the subsequent the laminated siltstone layer, typical of offshore transitional deposits. It could indicate that they were deposited under a lower energy than the previous one. The Manacapuru Formation is associated with a delta system in its lower part, whereas the shallow platform is recorded in the upper part (Carrozzi et al., 1973; Cunha et al., 2007; Rocha et al., 2019).

According to the lithological characteristics as described above, and the information provided by Tomassi et al. (2015a) and Tomassi et al. (2015b), in addition to the fossiliferous association of typical marine

brachiopods (Clarkson, 1992; Holmer and Popov, 2000), we locate the studied outcrops at the upper part of the Manacapuru Formation, attesting its typical shallow platform environment. According to the palynological analysis carried out by Grahn (2005) in the Belo Monte region, this portion is dated as Lochkovian.

4.1. Systematic paleontology

Class Lingulata Gorjansky and Popov, 1985.
Order Lingulida Waagen, 1885.
Superfamily Discinoidea Gray, 1840.
Family Discinidae Gray, 1840.
Genus *Orbiculoidea* d'Orbigny (1847).
Type species - *Orbicula forbesii* Davidson (1848).
Orbiculoidea baini Sharpe (1856).



Fig. 3. A–D: *Orbiculoidea baini* – A) MPEG- 3660 (ventral valve, internal mould), B) MPEG- 3660 (detail of the pedicle track), C) MPEG- 3657 (ventral valve, internal mould), and D) MPEG- 3662 (ventral valve, internal mould). E – F: *Orbiculoidea bodembenderi* – E) MPEG-3668 (ventral valve, external mould) and F) MPEG-3668 (detail of the rugellae in posterior margin). G – L: *Orbiculoidea excentrica* – G) MPEG-3689 (dorsal valve, external mould), H) MPEG-3690 (dorsal valve, countermould of MPEG-C9P1-4A), I) MPEG-3686 (dorsal valve, internal mould), J) MPEG-3672 (dorsal valve, internal mould), K) MPEG-3719 (ventral valve, internal mould), and L) MPEG-3720 (ventral valve, internal mould). Scale bar: 2 mm.

(Fig. 3. A – D).

1856 *Orbicula bainii* Sharpe, p. 210, pl. 26, Figs. 20–23.

1903 *Orbiculoidea baini* Sharpe Reed, p.168, pl. 20, Figs. 4–5.

1913 *Orbiculoidea baini* Sharpe Clarke, p. 301, pl. 25, Figs. 5–15.

1913 *Orbiculoidea baini* Sharpe Kozłowski, p. 8–108, pl. 1, Figs. 11–13.

1925 *Orbiculoidea (Roemerella) baini* Sharpe Reed, p. 36–38, pl. IV, Fig. 9–a.

1954 *Orbiculoidea baini* Sharpe Lange, p.33.

1967 *Orbiculoidea baini* Sharpe Davila and Rodriguez, p. 921–935.

1971 *Orbiculoidea baini* Sharpe Méndez-Alzola and Sprechmann, p. 517–525.

1985 *Orbiculoidea baini* Sharpe Melo, p. 48a–57a.

1991 *Orbiculoidea baini* Sharpe Figueiras, p. 57–64.

2001 *Orbiculoidea falklandensis* Sharpe Boucot et al., p. 111, pl. 2, Figs. 1–17.

2011 *Orbiculoidea baini* Sharpe Comniskey, p. 54–58, pl. 4–7.

2016 *Orbiculoidea baini* Sharpe Carbonaro and Ghilardi, p. 135–149, Fig. 6K.

2017 *Orbiculoidea baini* Sharpe Comniskey and Bosetti, p. 175–192, Fig. 3.3–3.4; 4.4–4.6.

2018 *Orbiculoidea baini* Sharpe Carbonaro et al., p. 11–20, Fig. 3.

Description: The ventral valve is flat, with a circular outline, width similar to length. Dimensions vary between 9.2 mm and 14.9 mm in length and 9.7 mm–15.1 mm in width. Rugellae well-marked, arranged concentrically around the apex. Valve flat with an apical region slightly depressed. Central apex with a smooth displacement towards the posterior region. The anterior region corresponds to approximately 60% of the valve. Between the posterior margin and the apex, it has on average between 15 and 17 well-marked rugellae, which thicknesses vary between 0.06 mm and 0.16 mm. The size of the interspaces between the growth lines has an almost imperceptible variation (0.18 mm–0.24 mm). Well-marked pedicle track, triangular in shape, starting behind the apical region and extending at least two-thirds of the length of the posterior region.

Occurrence: Sampling site C14P1, located at Sitio Belo Monte, municipality of Vitoria do Xingu, State of Para, Brazil. Manacapuru Formation (Lochkovian), Amazonas Basin.

Material: Ten ventral valves (MPEG- 3655 to MPEG-3664).

Remarks: The analyzed specimens show the diagnostic characteristics of the species, such as circular shell contour, well-marked rugellae, relatively large interspaces, eccentric apex, and well-marked pedicle track, similar to that was described by Sharpe (1856). The specimens of *Orbiculoidea baini* described by Clarke (1913), Lange (1954), Comniskey (2011), and Comniskey and Bosetti (2017) for the Devonian of the Parana Basin, differ in some aspects of the studied material, as they have more evident rugellae and larger pedicle track. The specimens analyzed in the present study are only larger than the specimens recorded by Comniskey et al. (2016), Comniskey and Bosetti (2017), and Carbonaro et al. (2018), that persisted after the lilliput effect (environmental stress), whose consequence is the decrease in the size of the species (phenotypes with maximum measures L: 7.0 W: 8.0).

Specimens from the Devonian of the Parana Basin have the pedicle track usually extended to the posterior margin; in the analyzed material only part of the pedicle track was preserved, which occupies about two-thirds of the length of the posterior region, making it difficult to compare with the other records in the literature. Boucot et al. (2001) described specimens from the Lower Devonian of the Parecis Basin, where the pedicle track is only one-third the length of the valve; despite this disparity, the authors choose not to propose a new species, justifying that such differences would be related to large-scale geographical variation, combined with others ecological aspects.

Geographic and stratigraphic distribution: South America: In Brazil, state of Parana, Parana Basin, Ponta Grossa and São Domingos formations (Pragian-Givetian) (Clarke, 1913; Lange, 1954; Comniskey and Bosetti, 2017); state of Goias, Alto Garças Sub-Basin, Chapada

Group Unit 4, (Givetian) (Carbonaro and Ghilardi, 2016; Carbonaro et al., 2018), and state of Mato Grosso, Parecis Basin, Pragian (Boucot et al., 2001). In Argentina, Argentine Pre-Cordillera, Talacasto Formation (Pragian) (Méndez-Alzola and Sprechmann, 1971); Bolivia, Pragian (Davila and Rodriguez, 1967); Falkland Islands, Fox bay Formation, Pragian (Sharpe, 1856), and Uruguay, Chacoparanense Basin, Cordobes Formation (Pragian) (Figueiras, 1991). Africa: South Africa, Bokkeveld Beds, Lower Devonian (Reed, 1925).

Orbiculoidea bodenbenderi Clarke (1913).

(Fig. 3. E – F).

1913 *Orbiculoidea bodenbenderi*, Clarke, p. 306, pl. 25, Figs. 16–22.

1954 *Orbiculoidea bodenbenderi* Clarke Lange, p. 41.

1985 *Orbiculoidea bodenbenderi* Clarke Melo, p. 58a.

1991 *Orbiculoidea bodenbenderi* Clarke Figueiras, p. 57–64.

2011 *Orbiculoidea bodenbenderi* Clarke Comniskey, p. 59–62, pl. 8–10.

2017 *Orbiculoidea bodenbenderi* Clarke Comniskey and Bosetti, p. 175–192, Figs. 3.7–3.8; 4.2; 4.7–4.9.

Description: The ventral valve is flat. Subcircular shell, 16.7 mm long and 16.3 mm wide; thinning in the contour of the posterior margin concerning the anterior margin; subcentral apex slightly shifted to the posterior margin; distance between the apex and the anterior margin is 11.8 mm, corresponding to approximately 70% of the total length of the valve; roughly evidenced rugellae, with thicknesses of 0.3 mm between the left part of the posterior margin and the apex. About 16 rugellae occur in the anterior region, in an interval of 5 mm. The spacing between rugellae is small and regular and the distance between them is approximately 0.7 mm. Unpreserved pedicle track.

Occurrence: Sampling site C14P1, located at Sitio Belo Monte, municipality of Vitoria do Xingu, State of Para, Brazil. Manacapuru Formation (Lochkovian), Amazonas Basin.

Material: Five ventral valves (MPEG-3665 to MPEG-3669).

Remarks: Clarke (1913) carried out the first description and discussion of the species *Orbiculoidea bodenbenderi* but did not give a diagnosis. We adopted the diagnosis proposed by Comniskey and Bosetti (2017), amended with minor modifications taken from the description made by Clarke (1913).

Besides *Orbiculoidea bodenbenderi* has the highest number of rugellae among the species identified herein, it has the same morphological characteristics of the specimens described by Comniskey and Bosetti (2017).

A break was observed extending from the apical region to the posterior margin (Fig. 3. E), responsible for not preserving the pedicle track.

Orbiculoidea bodenbenderi differs from *O. baini* in its quite flat ventral valve, due to the thinning in the contour of the posterior margin concerning the anterior margin, and in the number of rugellae that is larger, less evident, and with shorter spacing. *O. bodenbenderi* differs from *O. excentrica* because rugellae has a regular spacing, the apex is subcentral, and the number of rugellae is equal in both the anterior and posterior regions; in *O. excentrica* the spacing of the rugellae is irregular, the apex is subcentral, and the number of rugellae is greater in the anterior region.

Geographic and stratigraphic distribution: South America: In Brazil, state of Parana, Parana Basin, Ponta Grossa Formation (Pragian-Eifelian) (Clarke, 1913; Lange, 1954; Comniskey and Bosetti, 2017). Falkland Islands, Fox bay Formation, Pragian (Clarke, 1913); Uruguay, Chacoparanense Basin, Cordobes Formation, Pragian (Figueiras, 1991).

Orbiculoidea excentrica Lange (1943).

(Fig. 3. G – L).

1943 *Orbiculoidea excentrica*, Lange, p.223, pl. 17, Fig. 1.

1954 *Orbiculoidea excentrica* Lange Lange, p. 41–81.

1985 *Orbiculoidea excentrica* Lange Melo, p. 61, Fig. 1.

2011 *Orbiculoidea excentrica* Lange Comniskey, p. 63–65, pl.11.

2016 *Orbiculoidea excentrica* Lange Carbonaro and Ghilardi, p. 135–149, Fig. 6L.

2017 *Orbiculoidea excentrica* Lange Comniskey and Bosetti, p.

175–192, Fig. 3.5–3.6; 4.1.

2018 *Orbiculoidea excentrica* Lange Carbonaro et al., p. 11–20, Fig. 3C–D.

Description: Dorsal valve concave, subcircular in the outline. Posterior margin more acuminate than anterior margin. Dimensions vary between 3.2 mm and 9.9 mm in length and 3.6 mm–10.1 mm in width. Umbo elevated and conical. Inclination angle starts in the anterior margin towards the apex and is smaller when compared with the posterior region. Slope smoothly convex in the anterior region, and concave in the posterior region. Apex is submarginal, located near the posterior margin; the distance between the apex and the posterior margin of the dorsal valve is approximately 25%–30% of the total length of the valve. The tip of the apex is prominent, with a slight inclination towards the posterior margin. From the posterior margin towards the apex, it has an average of 19 rugellae, more concentrated in the anterior portion, generally seven more than the posterior part, with a thickness average of 0.02 mm–0.06 mm. The interspaces between the rugellae are irregular, varying between 0.12 mm and 0.26 mm, with the spacing being larger in the anterior region. The ventral valve is flat, subcircular in outline, and with a slight depression in the central portion. Submarginal apex displaced towards the posterior margin. Listrium present, covering completely the pedicle track.

Occurrence: Sampling sites C3P1, C9P1, C13P1, and C14P1, located at Sitio Belo Monte, municipality of Vitoria do Xingu, State of Para, Brazil. Manacapuru Formation (Lochkovian), Amazonas Basin.

Material: Forty-nine dorsal valves (MPEG-3670 to MPEG-3718) and three ventral valves (MPEG-3719 to MPEG-3721).

Remarks: Lange (1943) proposed this species based only on two specimens (ventral valves), and did not propose a diagnosis. Later, [Comniskey \(2011\)](#), [Comniskey and Bosetti \(2017\)](#), and [Carbonaro et al. \(2018\)](#), allowed a better comparison with the specimens studied herein. Then, we adopted the diagnosis of [Comniskey and Bosetti \(2017\)](#) adding an amendment including the characteristics proposed by [Lange \(1943\)](#).

The studied material presents the typical diagnostic characteristics of the species *Orbiculoidea excentrica*, such as submarginal apex, subcircular outline, great number of rugellae in the anterior region, and irregular spacing between them. However, the material described by [Lange \(1943\)](#) has almost twice rugellae in the anterior region, i.e., seven more rugellae in average than in the posterior region, when compared with the studied material. The distance from the apex to the posterior margin is very similar to the indicated by [Lange \(1943\)](#), and very close to the values stipulated by [Carbonaro et al. \(2018\)](#). The umbo is flatter and wider in some specimens (Fig. 3. J), which can be attributed to compaction during the fossilization process, or to interspecific variation. *Orbiculoidea excentrica* differs from *O. baini* in to the irregular spacing of the rugellae, the submarginal apex, and the pedicle track restricted to the apical region.

Geographic and stratigraphic distribution: This species is restricted to Brazil occurring in the states of Parana, Parana Basin, Ponta Grossa and São Domingos formations (Pragian and Givetian) ([Lange, 1943, 1954; Comniskey and Bosetti 2017](#)) and states of Goias, Alto Garças Sub-Basin, Chapada Group Unit 4, (Givetian) ([Carbonaro and Ghilardi, 2016; Carbonaro et al., 2018](#)).

Orbiculoidea xinguensis sp. nov.

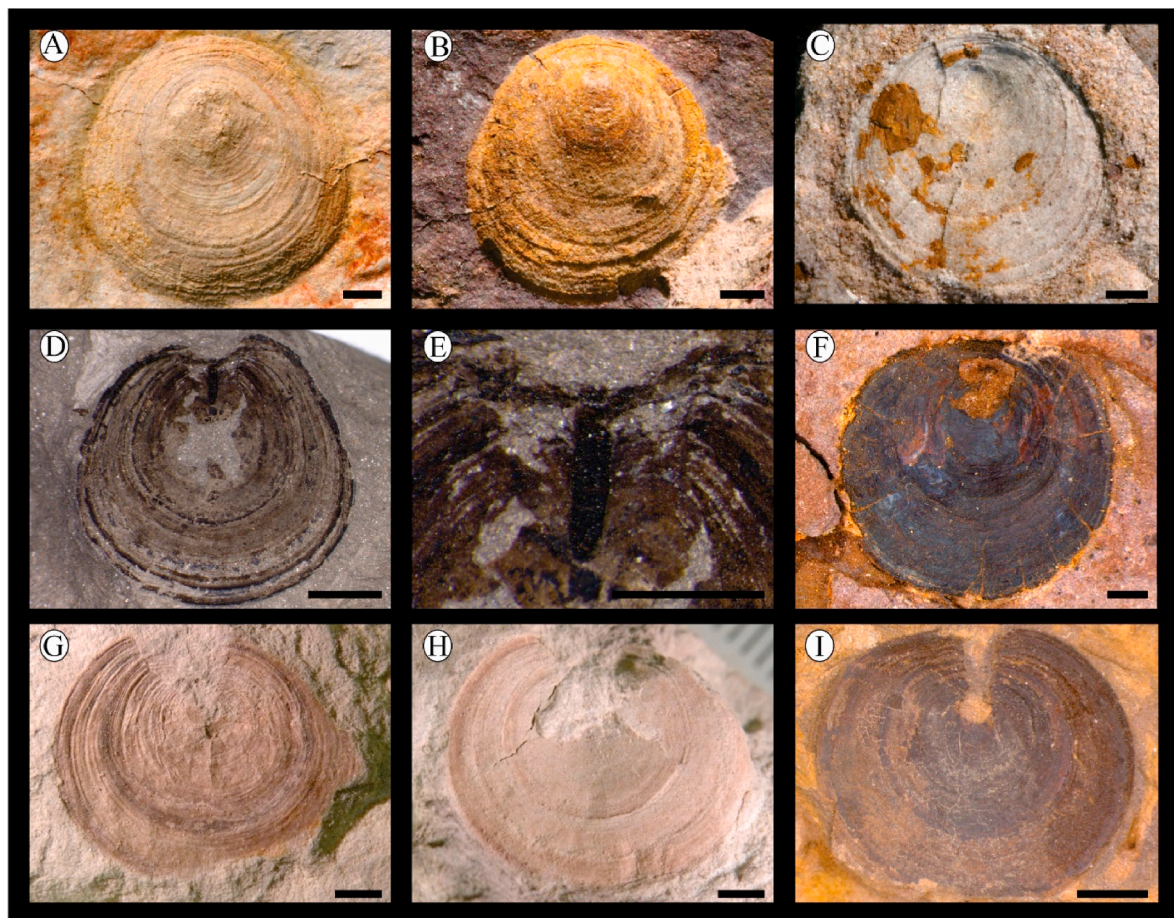


Fig. 4. A–D: *Orbiculoidea xinguensis* sp. nov. – A) MPEG-3729 (dorsal valve, external mould), B) MPEG-3723 (dorsal valve, external mould), C) MPEG-3735 (dorsal valve, external mould), D) MPEG-3740 (ventral valve, internal mould), and E) MPEG-3740 (detail of the pedicle track). F–I: *Orbiculoidea katzeri* sp. nov. – F) MPEG-3746 (dorsal valve, internal mould), G) MPEG-3759 (dorsal valve, external mould), H) MPEG-3758 (dorsal valve, external mould), and I) MPEG-3760 (ventral valve, internal mould). **Scale bar:** A), B), C), D), F), G), H), and I): 2 mm; E): 1 mm.

(Fig. 4. A – E, Fig. 5. A – D).

Diagnosis: Convex flat shell, almost subtriangular in outline. The anterior margin is broader than the posterior margin. Dorsal valve high and convex, umbo well marked. Apex flattened, submarginal, displaced towards the posterior margin. The ventral valve is flat, with a slight elevation in the umbo region. Listrium short, cylindrical, covering the pedicle track completely. Thin rugellae, with small and regular interspaces arranged in both valves.

Etymology: After “*xinguensis*”, referring to river Xingu, a famous river in the Amazon region, the main river of the studied area, Belo

Monte.

Holotype: Dorsal valve (MPEG-3729).

Paratypes: Four dorsal valves (MPEG-3723, MPEG-3726, MPEG-3728, and MPEG-3735). One ventral valve (MPEG-3740).

Description: Shell subtriangular in outline. The dorsal valve is high, convex, and obtusely sub-conical. Dimensions vary between 9.2 mm and 17.8 mm in length and 8.8 mm–18.1 mm in width. The apical region is well marked and elevated with a concave slope extending from the apex to the anterior margin. Apex flattened, slightly elevated, submarginal, displaced towards the posterior margin. On average, the anterior region

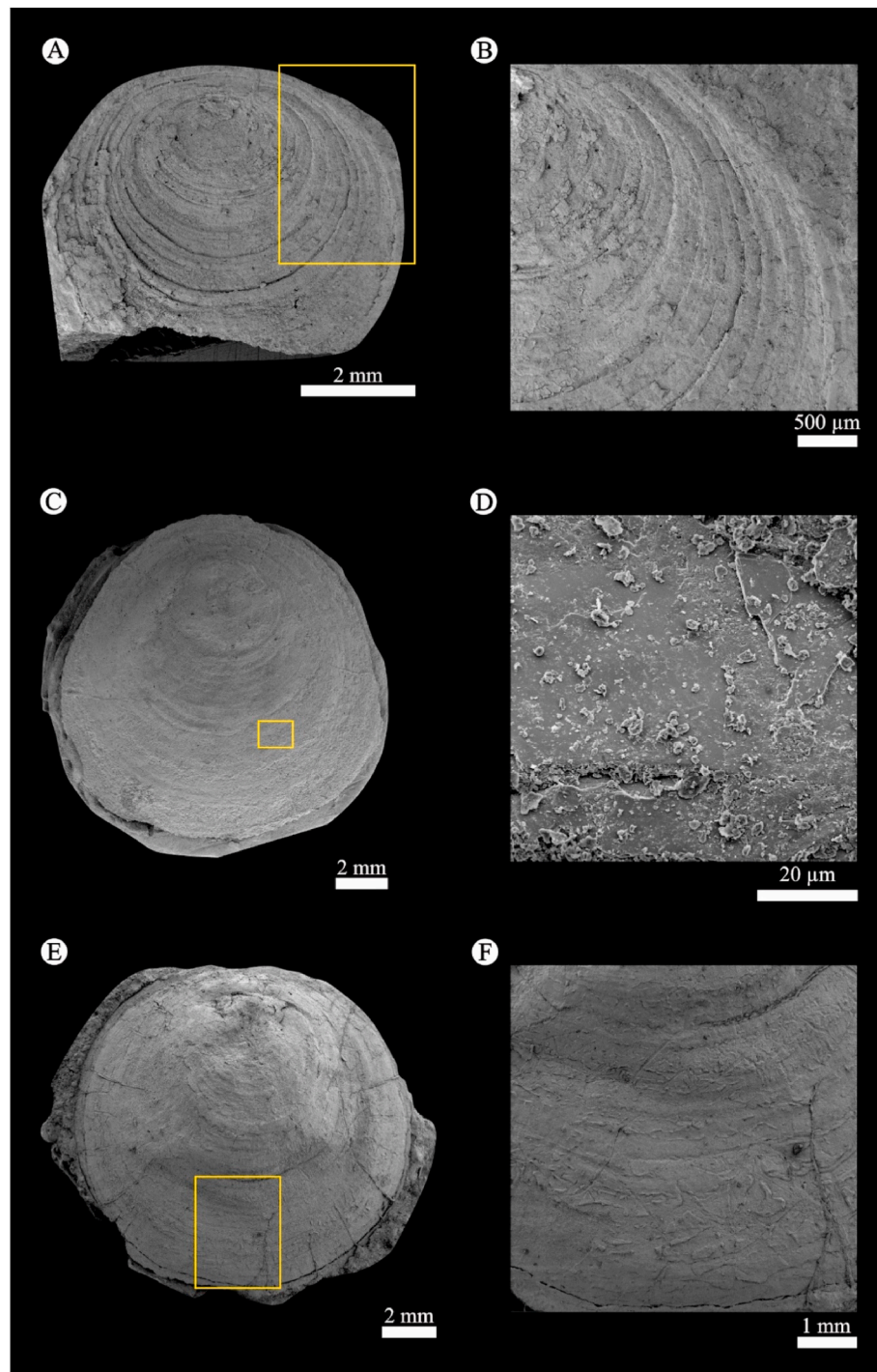


Fig. 5. SEM images. A – D: *Orbiculoidea xinguensis* sp. nov. – A) MPEG-3726 (dorsal valve, external mould), B) MPEG-3726 (rugellae well-marked, with regular interspaces), C) MPEG-3728 (dorsal valve, external mould), and D) MPEG-3728 (absence of micro ornamentation). E – F: *Orbiculoidea katzeri* sp. nov. – E) MPEG-3746 (dorsal valve, internal mould) and F) MPEG-3746 (absence of micro ornamentation).

corresponds to approximately 80% of the valve area. The rugellae are thin, well-marked, arranged concentrically around the apex. On the posterior margin towards the apex, it has an average of 22 rugellae, with small and regular interspaces. The ventral valve is flat, with a slight depression in the umbo region. Submarginal apex, displaced in the posterior direction. Umbo is well marked and flat. Well-marked rugellae, with regular interspaces. Pedicle track short and cylindric.

Occurrence: Sampling sites C3P1, C13P1, and C14P1, located at Sitio Belo Monte, municipality of Vitoria do Xingu, State of Para, Brazil. Manacapuru Formation (Lochkovian), Amazonas Basin.

Material: Seventeen dorsal valves (MPEG-3722 to MPEG-3738) and four ventral valves (MPEG-3739 to MPEG-3742).

Remarks: The specimens described herein have morphological characteristics similar to the *Gigadiscina collis* ones described in [Comniskey \(2011\)](#) and [Comniskey and Bosetti \(2017\)](#), such as the subtriangular outline, thin rugellae with small spacing, and high dorsal valve. The microstructural analysis through electronic scanning microscope showed the absence of pores on the surface of both valves (Fig. 5. C – D), a typical characteristic of the genus *Gigadiscina*. Besides, the analyzed specimens are very small when compared to *Gigadiscina*, when the large size of the valves was one of the main reasons for the creation of this genus.

Among the characteristics of *Orbiculoidea xinguensis* sp. nov., stands out the anterior margin, which is much larger than the posterior margin, resulting in a subtriangular outline, not common in *Orbiculoidea* species, in which predominate circular to subcircular outlines.

Orbiculoidea xinguensis sp. nov. differs from *O. baini* in its subtriangular outline, submarginal apex, and rugellae with smaller interspaces. It also differs from *O. bodenbenderi* in the submarginal apex, subtriangular outline, and by a slight depression in the central region of the ventral valve, whereas in *O. bodenbenderi* the apex is central to subcentral, subcircular outline, and flat ventral valve. It differs from *O. excentrica* due to its flatter apex, thinner rugellae with regular spacing; in *O. excentrica* the apex is conical and high, the rugellae are well marked and with irregular spacing.

Orbiculoidea katzeri sp. nov.

(Fig. 4. F–I, Fig. 5. A – D).

Diagnosis: Subcircular shell, valve wider than long. Dorsal valve marginally flat, quite high and marked in the umbo region. Umbo high. Apex flattened, subcentral, slightly detached towards the posterior margin. Ventral valve flattened in the margins, with a slight elevation in the umbonal region. Listrium, robust, covering completely the pedicle track. Rugellae thin, with small and regular spacings.

Etymology: After “katzeri”, a tribute to geologist and paleontologist Friedrich Katzer, for his prominent contributions to paleontological studies in Amazonia during the 19th century.

Holotype: Dorsal valve (MPEG-3746).

Paratypes: Two dorsal valves (MPEG-3759 and MPEG-3758). One ventral valve (MPEG-3760).

Description: Dorsal valve convex and with subcircular outline. Dimensions vary between 9.6 mm and 19.8 mm in length and 10.1 mm–19.8 mm in width. The width measurements are considerably larger when compared to the length measurements. Broad anterior margin. Rugellae well-marked. Apex robust, subcentral, slightly displaced towards the posterior margin. Umbonal region well marked and elevated, making the shell convex. Ventral valve flat, with a slight depression in the umbonal region, and subcircular outline. Apex flattened, subcentral, slightly displaced to the posterior margin. Umbonal region with a slight depression. Rugellae very evident, slightly accentuated, most notable in the lateral part of the posterior margin. Pedicle track robust, cylindrical in shape, starting from the apex to the posterior margin.

Occurrence: Sampling site C14P1, located at Sitio Belo Monte, municipality of Vitoria do Xingu, State of Para, Brazil. Manacapuru Formation (Lochkovian), Amazonas Basin.

Material: Seventeen dorsal valves (MPEG-3743 to MPEG-3759) and

one ventral valve (MPEG-3760).

Remarks: Some characteristics are quite striking in the analyzed specimens, such as width, which is considerably greater than length, giving the impression that the contours of the valves are flattened, which differs from all the other species previously described, and the robust pedicle track, reaching the posterior margin.

Orbiculoidea katzeri sp. nov. differs from *O. baini* in the subcircular outline, more robust umbo, and rugellae with short spacing; in *O. baini* the outline is circular, the umbo is smaller and the spacing between the rugellae is larger. It differs from *O. excentrica* because of the umbo, which is robust and flattened, and the apex, which is subcentral, whereas in *O. excentrica* the umbo is smaller, the apex is conical, higher, and submarginal. It differs from *O. xinguensis* sp. nov. due to its subcircular outline and robust pedicle track, while in *Orbiculoidea xinguensis* sp. nov. the outline is subtriangular and the pedicle track is small.

5. Discussion

5.1. Paleoeological aspects

Discinoids are brachiopods with two valves of organophosphate composition, predominantly marine, occurring in shoreface to offshore deposits ([Holmer and Popov, 2000](#); [Comniskey et al., 2016](#)). *Orbiculoidea* lived a mostly in the neritic zone ([Zhang et al., 2018](#)). The family Discinidae has different life habits, which brought up several discussions; more recent research suggests epibenthic habit ([Südkamp, 1997](#); [Mergl, 2001](#)). The discinoids identified in the present work (*Orbiculoidea baini*, *O. bodenbenderi*, *O. excentrica*, *O. xinguensis* sp. nov., and *O. katzeri* sp. nov.) have flat or slightly arched ventral valves (described in the topic Paleontological Systematics), which indicates that they were attached to the substrate mainly by the pedicle, with an epibenthic habit ([Mergl, 2001](#)).

The analyzed material consists mostly of disarticulated valves. According to [Südkamp \(1997\)](#), the fact that inarticulate brachiopods have both valves connected only by muscles explains why the valves are commonly preserved disarticulated.

Studies on the habits of living genera of the Superfamily Discinoidea (*Discina* Lamarck, 1819; *Disciniscia* Dall, 1871; *Discradisca* Stenzel, 1964; *Pelagodiscus* Dall, 1908) are used as parameters to infer the life habits of fossil discinoids, even having a significant temporal distance ([Zhang et al., 2018](#)).

Orbiculoidea lived mostly in shallow coastal marine environments. This statement is suggested by the fact that the distribution of most recent discinoids occurs at depths less than 30 m ([Emig, 1997](#); [Zhang et al., 2018](#)). According to [Zhang et al. \(2018\)](#), most *Orbiculoidea* fossil records (92.7%) indicate shallow marine conditions. The discinoid fauna recorded in the Devonian of the Parana Basin, is associated with platform marine deposits ([Comniskey, 2011](#); [Comniskey et al., 2016](#); [Comniskey and Bosetti, 2017](#)).

In the present study the *Orbiculoidea* species that occur in fine-grained massive sandstone interspersed with clay lenses, and in the fine-grained sandstone with incipient lamination, are associated with shoreface deposits. On the other hand, the discinoids that occur along with rhynchonelliforms in the base of the laminated siltstone are associated with offshore transitional deposits. Therefore, the presence of *Orbiculoidea* in the Manacapuru Formation suggests a shallow marine environment, corroborating previous studies concerning the upper part of this formation ([Carrozzi et al., 1973](#); [Cunha et al., 2007](#); [Rocha et al., 2019](#)).

When analyzing the discinoids identified in the present research we realize that they have morphological characteristics of adult forms; however, when we compare their sizes with the other records in the literature ([Méndez-Alzola and Sprechmann, 1971](#); [Boucot et al., 2001](#); [Comniskey and Bosetti, 2017](#)), we note that they are relatively small. The exception are *O. baini* and *O. excentrica* specimens from the Givetian of the Unit 4 of the Alto das Garças Sub-basin (Parana Basin) and the

Upper part of the São Domingos Formation, Parana Basin (Comniskey et al., 2016; Comniskey and Bosetti, 2017; Carbonaro et al., 2018), whose reduced size is related to a global biotic crisis “Kačák”, which occurred in the transition Eifelian/Givetian (House, 1996, 2002; Bosetti et al., 2010; Horodyski et al., 2014; Comniskey et al., 2016; Comniskey and Bosetti 2017).

According to Boucot et al. (2001) morphological variations among some species of *Orbiculoidea* would be related to geographical variation in large scale, combined with ecological factors. Chuang (1961) demonstrated the relationship between local environmental effects and the growth rate of lingulids. The fact that the registered fauna has small sizes may be linked to paleobiogeographic factors and consequently environmental changes (for more detail see discussion below in the *Stratigraphic and paleobiogeographic distribution* chapter).

5.2. Stratigraphic and paleobiogeographic distribution

Orbiculoidea has a wide geographical distribution (Africa, North America, South America, Antarctica, Asia, Europe, and Oceania) but a restricted stratigraphic range (Ordovician to Permian). The survey of its geographic occurrence allowed to verify that despite the presence of *Orbiculoidea bairni* in Pragian strata of South Africa (Reed, 1925), it has the widest geographic and stratigraphic distribution in South America (Fig. 6). *Orbiculoidea bodenbenderi* is registered only in South America, in the Pragian to Eifelian interval, whereas *O. excentrica* is registered only in Brazil, occurring in the Pragian to Emsian of the Paraná Basin. During the Eifelian there is no record of *O. excentrica*; however, it is recorded in

the Givetian of the Paraná Basin and Alto das Garças sub-basin.

The record of the species *Orbiculoidea bairni*, *O. bodenbenderi*, and *O. excentrica* in marine facies of the Manacapuru Formation make it the oldest record of South America (Lochkovian). Although *Orbiculoidea* has already been briefly mentioned in the literature in the Manacapuru Formation, this is the first record of *O. bairni*, *O. bodenbenderi*, and *O. excentrica* in the Manacapuru Formation, and is also the first occurrence for Northern Brazil.

An important point regarding the *Orbiculoidea* geographical expansion during the Devonian, is Emig's (1997) claim that modern inarticulate brachiopod, have their distribution controlled by environmental factors, and not by the dispersion potential of their larvae. Zhang et al. (2018) demonstrated that the distribution of *Orbiculoidea* throughout the Paleozoic would be related to global climate changes and the geographical configuration of continental masses.

Orbiculoidea appeared in the Upper Ordovician, in shallow seas of regions located in low latitudes (South Baltic, West Bank of Gondwana, and in Laurasia) with relatively warm temperatures (Zhang et al., 2018). In the Late Ordovician to Early Silurian (Fig. 7. A), the Hirnantian Glaciation occurred, which persisted for almost 35 million years (Finnegan et al., 2011). Climatic conditions were quite severe in Gondwana, with the persistence of only a few discinoids, such as *Kosoidea australis*, from the Iapó and Vila Maria formations (Parana Basin), recorded by Zabini et al. (2019). During the Silurian, post-glacial warming was slow in Gondwana, and the environmental conditions were very unstable (Torsvik and Cocks, 2013), disfavoring *Orbiculoidea* colonization in this region. Much of the *Orbiculoidea* records are limited to low latitudes

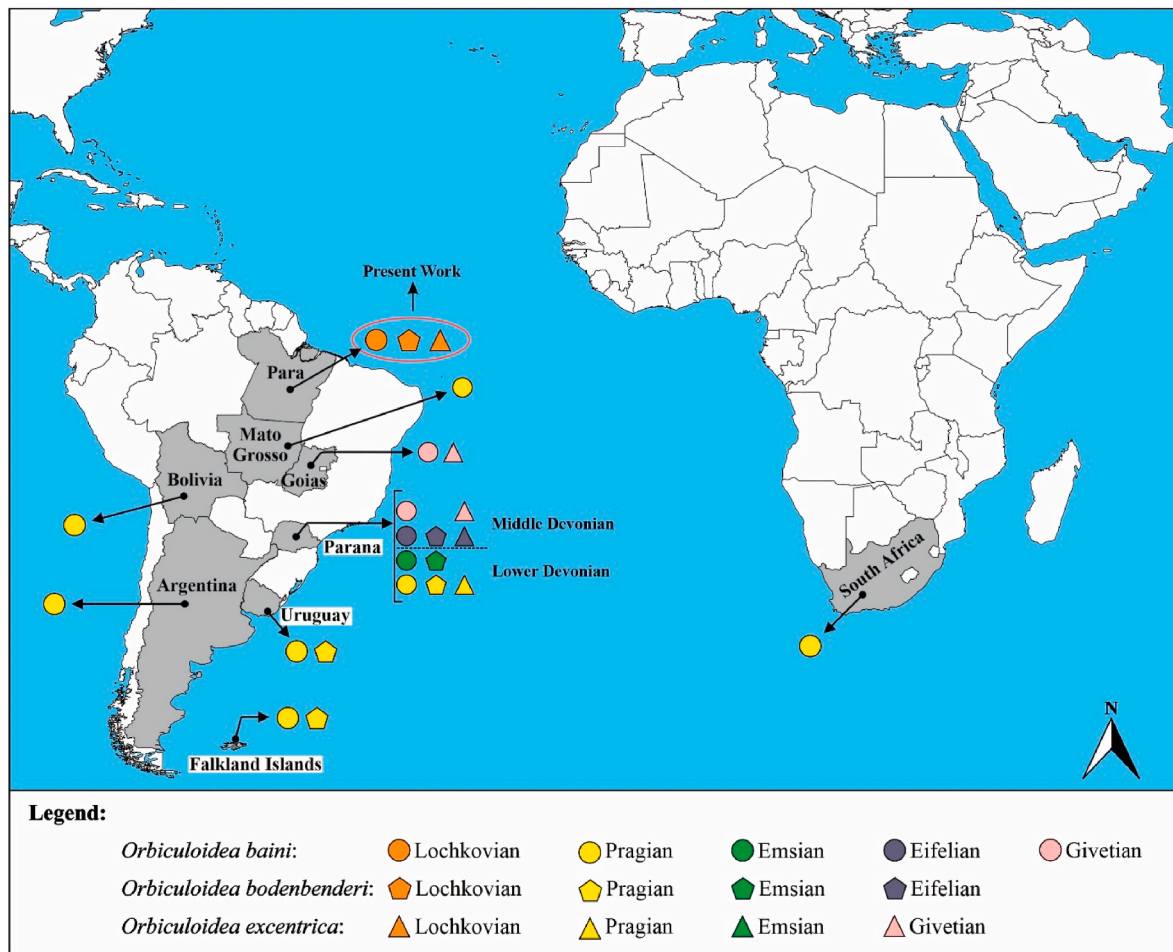


Fig. 6. Geographic distribution of *Orbiculoidea bairni*, *Orbiculoidea bodenbenderi*, and *Orbiculoidea excentrica*. Source: author.

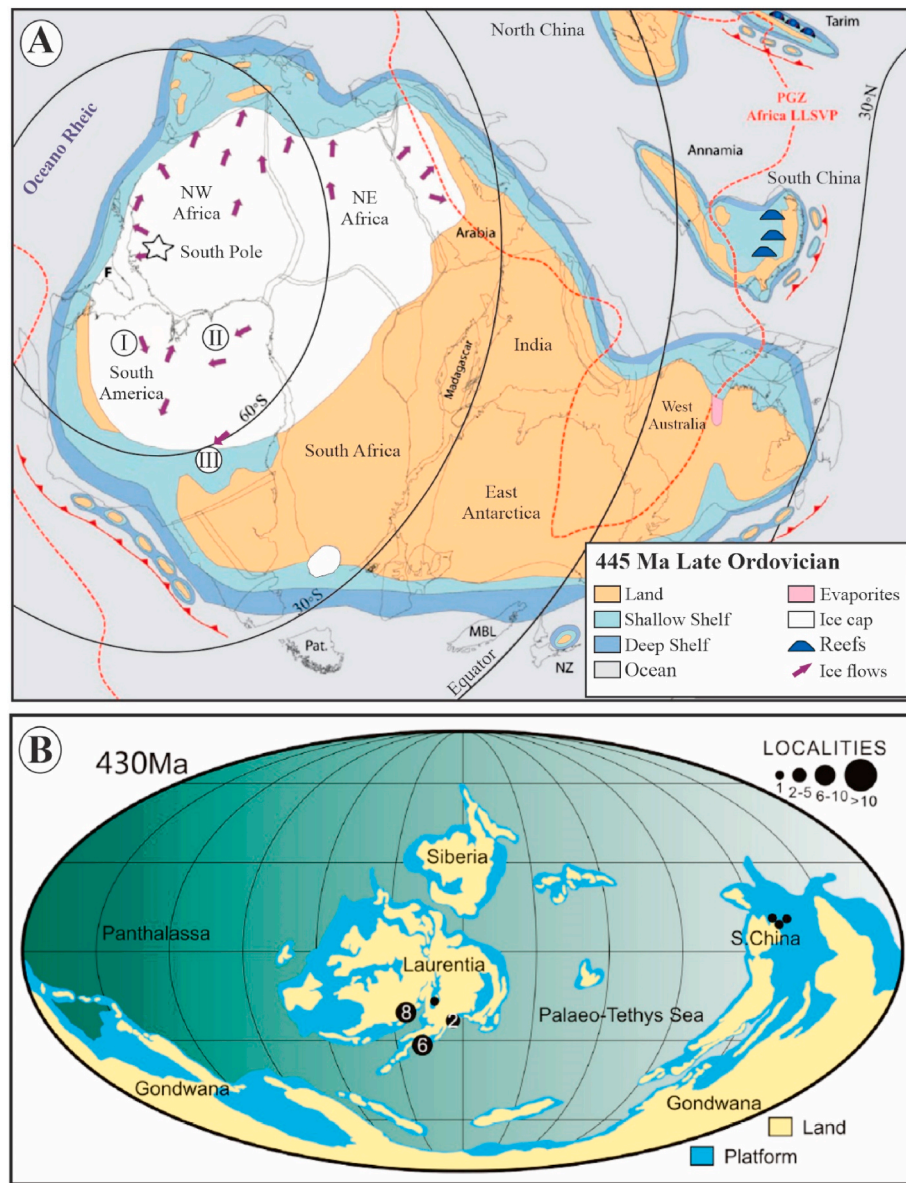


Fig. 7. A) Gondwana 445 Ma paleogeographic arrangement. I) Amazonas Basin; II) Parnaíba Basin; III) Parana Basin. B) Distribution of the *Orbiculoidea* during the Silurian (430 Ma); black numbers and circles represent the number of occurrences. Source: A) modified from Torsvik and Cocks (2013); B) modified from Zhang et al. (2018).

(part of Laurasia and southern China) (Fig. 7. B).

The paleobiogeographic distribution of *Orbiculoidea* expanded significantly to high latitudes during the Lower Devonian (Fig. 8. B), especially in Gondwana (Zhang et al., 2018). This migration is linked to two factors: the main continental blocks (Laurasia and Gondwana) were close enough to allow the larvae of invertebrates (*Orbiculoidea*) to cross the oceans more easily (Torsvik and Cocks, 2013; Zhang et al., 2018) (Fig. 8. A).

The other factor is that during the transition from the Silurian to the Devonian, occurred the melting of the polar ice caps that covered part of Africa and South America, resulting in marine transgressions that reached a large part of the supercontinent Gondwana, mainly the northwest portion (Carozzi et al., 1973; Caputo, 1984; Johnson, 2006; Torsvik and Cocks, 2013). Such conditions were fundamental for the significant paleogeographic distribution of brachiopods in Gondwana during the Devonian.

These transgressions associated with the approximation of the continental masses and to less severe temperatures when compared to

the Early Silurian, were probably one of the factors that caused a notable increase in the shallow water benthic faunas in Gondwana (Boucot and Blodgett, 2001; Torsvik and Cocks, 2013; Zhang et al., 2018).

During the Lochkovian (Lower Devonian), the siliciclastic sediments of the upper portion of the Manacapuru Formation (Amazonas Basin) were deposited in a shallow platform environment (Carozzi et al., 1973; Cunha et al., 2007; Rocha et al., 2019). The Amazonas Basin was closer to Laurasia, the environmental conditions were marine, the climate was not as severe as at the beginning of the Silurian, and these conditions probably enabled the migration of *Orbiculoidea* larvae from Laurasia to the Amazonas Basin first, as shown by the records of *O. bairi*, *O. bodenbenderi*, and *O. excentrica* in strata of the Manacapuru Formation shown in the present work.

The siliciclastic rocks of the Furnas Formation register the Lower Devonian in the Parana Basin, with a complex depositional environment, that generated a great number of debates (Milani et al., 2007). Many authors suggest shallow marine conditions (Petri, 1948; Sanford and Lange, 1960; Bigarella et al., 1966; Lange and Petri, 1967; Bigarella,

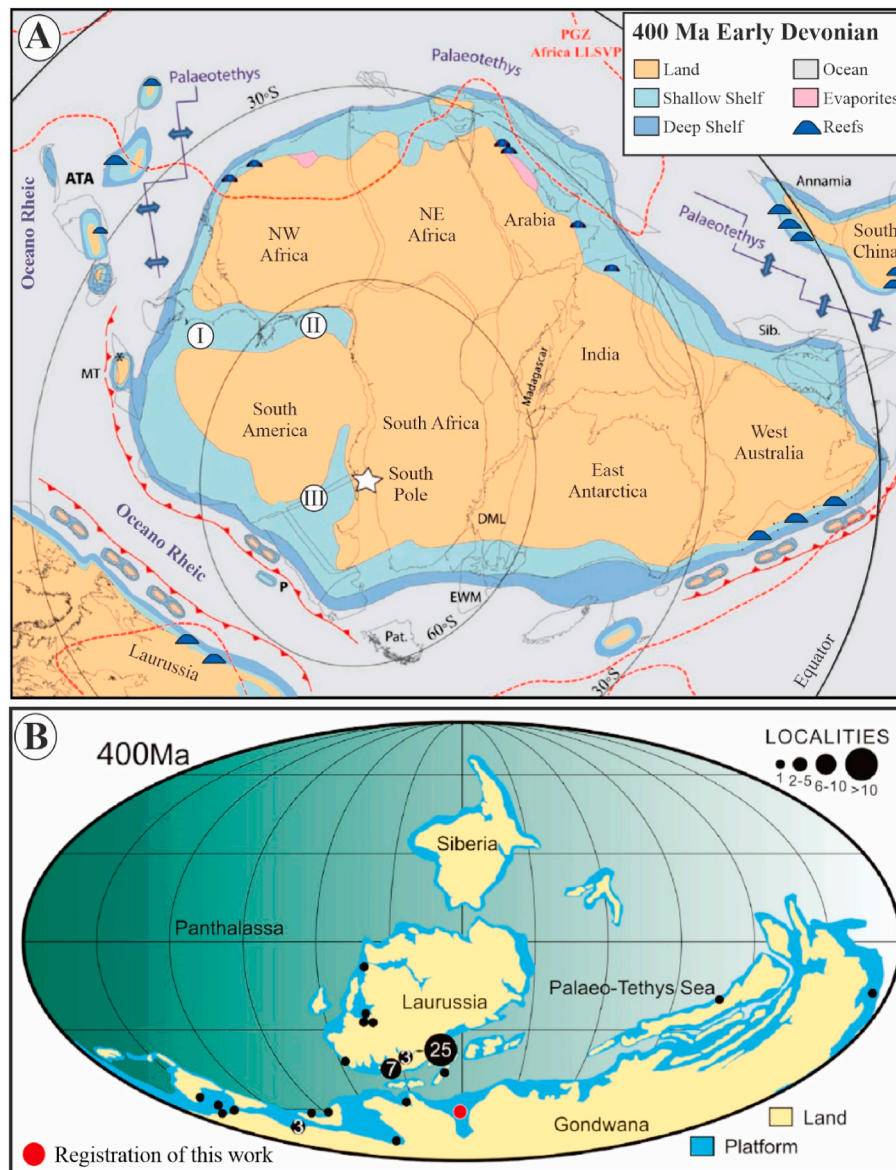


Fig. 8. A) Gondwana 400 Ma paleogeographic arrangement. I) Amazonas Basin; II) Parnaíba Basin; III) Parana Basin. B) Distribution of the *Orbiculoidea* during the Lower Devonian (400 Ma); black numbers and circles represent the number of occurrences. Source: A) modified from Torsvik and Cocks (2013); B) modified from Zhang et al. (2018).

1973). Northfleet et al. (1969), Schneider et al. (1974), Andrade and Camarço (1980), Melo (1988). On the other hand, Zalán et al. (1987) point to a fluvial origin; while Bergamaschi (1992) and Assine et al. (1994) indicate deltaic and marine platform conditions. Nevertheless, what we do know is that there is no occurrence of *Orbiculoidea* recorded in the literature for this interval.

Subsequently, in the Pragian (Ponta Grossa Formation), with the establishment of marine conditions (shallow platform), there are the first occurrences of *Orbiculoidea bairni*, *O. bodenbenderi*, *O. excentrica*, *Gigadiscina collis*, and *Rugadiscina stagona* in strata of the Parana Basin (Clarke, 1913; Lange, 1943, 1954; Comniskey and Bosetti, 2017). This diverse fauna was more abundant during the end of Pragian and the beginning of Emsian (Comniskey and Bosetti, 2017).

At the end of Emsian, there was a decline in the distribution and abundance of the discinoids of the Devonian of the Parana Basin. Species such as *Orbiculoidea bodenbenderi*, *Gigadiscina collis*, and *Rugadiscina stagona*, in addition to other organisms belonging to the Malvinokaffric Realm, were no longer found in sedimentary successions (Bosetti et al., 2012; Comniskey and Bosetti, 2017).

Horodyski et al. (2014) detected evidence of the global Kačák Eifelian/Givetian transition event in the Parana Basin. The Kačák event is associated with a transgressive peak which would have resulted in drastic environmental changes, such as changes in temperature and a period of global anoxia, which would have affected primary production (House, 1996, 2002).

This biotic crisis resulted in the extinction of a large part of the discinoids in the Devonian. *Orbiculoidea bairni* and *O. excentrica* are described with reduced sizes (90% smaller) in the Givetian strata of the São Domingos Formation. This drastic reduction in size of these discinoids is a consequence of the Lilliput Effect (Bosetti et al., 2010; Comniskey et al., 2016; Comniskey and Bosetti 2017). There are no occurrences of discinoids in the younger units, indicating that the discinoids disappeared in the Givetian (Late Devonian) (Comniskey et al., 2016).

6. Conclusions

The taxonomical study of the Brachiopoda (Discinoidea) from Belo

Monte, municipality of Vitoria do Xingu, State of Pará, allowed to recognized five species of *Orbiculoidea*: *Orbiculoidea baini*, *O. bodenbenderi*, *O. excentrica*, and two new species described herein *O. xinguensis* sp. nov. and *O. katzeri* sp. nov. These are the first records of the species *O. baini*, *O. bodenbenderi*, and *O. excentrica* in the Manacapuru Formation, and also the first occurrences for Northern Brazil. This Early Devonian discinoids association is the oldest of South America.

The presence of discinoids in the strata of the Manacapuru Formation suggests a shallow marine environment, corroborating the environment proposed earlier for the upper part of that formation. Their occurrences in the transition of sandstones to finer laminated siltstones layers indicate that they were deposited under high to low energy. It corroborates that the discinoids have preference for shallow water. This group has been recorded also in sandstones and siltstones of the São Domingos and Ponta Grossa formations, Parana Basin.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

The authors would like to thanks the Museu Paraense Emilio Goeldi (MPEG) for the infrastructure provided by the laboratories of the Coordenação de Ciências da Terra e Ecologia. The Federal University of Pará (UFPA) supported this research through the Programa de Pós Graduação em Geologia e Geoquímica (PPGG), and to Sergio Agustín Martínez Chiappara for the valious contribution to the language review and comments. This work was carried out with the support of the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior-Brazil (CAPES) – financing code 001.

References

- Almeida, F.F.M., 1967. Origem da plataforma brasileira, vol. 241. Boletim da divisão de Geologia e Mineralogia, Rio de Janeiro, p. 36.
- Andrade, S.M., Camargo, P.E.N., 1980. Estratigrafia dos sedimentos devonianos do flanco nordeste da Bacia do Paraná. In: 31^o Congresso Brasileiro de Geologia, Camboriú, vol. 5, pp. 2828–2836.
- Assine, M.L., Soares, P.C., Milani, E.J., 1994. Sequências tectono-sedimentares Meso-Paleozoicas da Bacia do Paraná, Sul do Brasil. Rev. Bras. Geociências 24, 77–89.
- Bergamaschi, S., 1992. Análise sedimentológica da Formação Furnas na faixa de afloramentos do flanco norte do arco estrutural de Ponta Grossa, Bacia do Paraná, Brasil. Master's Dissertation. Geology Federal University of Rio de Janeiro, Rio de Janeiro, pp. 1–172.
- Bigarella, J.J., 1973. Paleocorrentes e deriva continental (comparação entre África e América do Sul). Bol. Parana. Geocienc. 31, 141–224.
- Bigarella, J.J., Salamuni, R., Marques, F.L.P., 1966. Texturas e estruturas da Formação Furnas e sua significação paleogeográfica. Boletim da Universidade Federal do Paraná 18, 1–114.
- Bosetti, E.P., Horodyski, R.S., Zabini, C., Matsumura, W.M.K., Penteado, A.C., 2010. Ocorrência de fenótipos subnormais no topo da Formação Ponta Grossa (Devoniano), Tibagi, estado do Paraná, Brasil: implicações tafonômicas e Paleossinecológicas. Bol. Mus. Para. Emilio Goeldi 5 (2), 135–149.
- Bosetti, E.P., Grahn, Y., Horodyski, R.S., Mauller, P.M., 2012. The first recorded decline of the Malvinokaffric Devonian fauna in the Paraná Basin (southern Brazil) and its cause; taphonomic and fossil evidences. J. S. Am. Earth Sci. 37, 228–241.
- Boucot, A.J., Blodgett, R.B., 2001. Silurian-Devonian biogeography. In: Brunton, C.H.C., Cocks, L.R.M., Long, S.L. (Eds.), Brachiopods Past and Present. Taylor and Francis, London, pp. 335–344.
- Boucot, A.J., Rowell, A.J., Racheboeuf, P., Pereira, E., Melo, J.H.G., Siqueira, L.P., 2001. Position of the Malvinokaffric Realm's northern boundary (Early Devonian) based on newly discovered brachiopods from the Parecis Basin (Brazil). J. Czech Geol. Soc. 46, 109–120.
- Caputo, M.V., 1984. Stratigraphy, Tectonics, Paleoclimatology and Paleogeography of Northern Basins of Brazil. Phd Thesis, Universidade da California, pp. 1–603.
- Caputo, M.V., Crowell, J.C., 1985. Migration of glacial centers across Gondwana during paleozoic era. Geol. Soc. Am. Bull. 96 (8), 1020–1036.
- Caputo, M.V., Rodrigues, R., Vasconcelos, D.N.N., 1971. Litoestratigrafia da Bacia do Amazonas. Relatório Técnico Interno. 641-A, pp. 35–46. Petrobras-Renor.
- Carbonaro, F.A., Comniskey, J.C., Corral, H.S., Ghilardi, R.P., 2018. *Orbiculoidea baini* and *Orbiculoidea excentrica* (Brachiopoda, Discinidae) from the middle devonian (Alto Garças sub-Basin, Paraná Basin) of caiaipônia, goiás (Brazil). Geologia USP. Série Científica 18 (4), 11–20.
- Carbonaro, F.A., Ghilardi, R.P., 2016. Fósseis do devoniano de Goiás, Brasil (sub bacia Alto Garças, bacia do Paraná). Papéis Avulsos Zool. (São Paulo) 56 (11), 135–149.
- Carozzi, A.V., Pamplona, H.R.P., Castro, J.C., Contreiras, C.J.A., 1973. Ambientes Depositionais e Evolução Tecto-sedimentar da Seção clástica Paleozoica da Bacia do Médio Amazonas. In: Anais do 28^o Congresso Brasileiro de Geologia. Aracaju, pp. 279–314.
- Chuang, S.H., 1961. Growth of the postlarval shell in *Lingula unguis* (L.) (Brachiopoda). Proc. Zool. Soc. Lond. 137, 299–310.
- Clarke, J.M., 1913. Fósseis Devonianos Do Paraná, vol. 1. Monographias do Serviço Geológico e Mineralógico do Brasil, Rio de Janeiro, pp. 1–353.
- Clarkson, E.N.K., 1992. Invertebrate Palaeontology and Evolution, vol. 3. Chapman & Hall, p. 153.
- Comniskey, J.C., Bosetti, E.P., 2017. Discinoids of the malvinokaffric realm: stratigraphic, paleogeographical distribution and systematic review. Terr@Plural 11 (2), 175–192.
- Comniskey, J.C., Bosetti, E.P., Horodyski, R.S., 2016. Taphonomic aspects and the lilliput effect on devonian discinoids of the Paraná Basin, apucarana sub-Basin. Brazil. Gaea: J. Geosci. 9 (1), 55–64.
- Comniskey, J.C., 2011. Paleontologia dos Discinidae (Brachiopoda: Linguliformea) da sucessão devoniana da Bacia do Paraná, Estado do Paraná, Brasil: Revisão Sistemática, distribuição geográfica e estratigráfica. Ponta Grossa, Paraná. Master's Dissertation. Geology State University of Ponta Grossa, pp. 1–179.
- Cunha, P.R.C., Gonzaga, F.G., Coutinho, L.F.C., Feijó, F.J., 1994. Bacia do Amazonas. Bol. Geociências Petrobras 8, 47–55.
- Cunha, P.R.C., Melo, J.H.G., Silva, O.B., 2007. Bacia do Amazonas. Bol. Geociências Petrobras 15, 227–251.
- d'Orbigny, A., 1847. Considérations zoologiques et géologiques sur les Brachiopodes ou Palliobranches. Comptes Rendus hebdomadaires des Séances de l'Académie des Sciences 25 (7), 266–269.
- Davidson, T., 1848. Mémoire sur les brachiopodes du Système silurien supérieur de l'Angleterre. Bulletin de la Société géologique de France, série 2 (5), 370–374.
- Davila, J., Rodriguez, E., 1967. The Devonian System in Bolivia and the problem of its base. In: International symposium Devonian System, 2, pp. 921–935.
- Emig, C.C., 1997. Ecology of inarticulated brachiopods. In: Kaesler, R.L. (Ed.), Treatise on Invertebrate Paleontology. Part H. Brachiopoda 1 (Revised). Geological Society of America & University of Kansas Press, pp. 473–495.
- Figueiras, A., 1991. Fauna eodevónica del Uruguay. Revista Técnica da YPF 12 (1), 57–64.
- Finnegan, S., Bergmann, K., Eiler, J.M., Jones, D.S., Fike, D.A., Eisenman, I., Hughes, N. C., Tripathi, A.K., Fisher, W.W., 2011. The magnitude and duration of late Ordovician-early Silurian glaciation. Science 331 (6019), 903–906.
- Fonseca, V.M.M., Ponciano, L.C.M.O., 2011. Braquiópodes do Devoniano Médio das bacias do Amazonas e Parnaíba. In: Carvalho, I.S. (Ed.), Paleontologia: Cenários de Vida, vol. 1. Editora Interciência, Rio de Janeiro, pp. 169–190, 4.
- Gorjansky, V.I.U., Popov, L.E., 1985. Morphology, systematic position and origin of the inarticulate brachiopods with calcareous shells. Paleontologicheskii Zhurnal 3, 3–14.
- Grahn, Y., 2005. Silurian and lower devonian chitinozoan taxonomy and biostratigraphy of the Trombetas group, Amazonas Basin, northern Brazil. Bulletin of Geosciences, Prague 80 (4), 245–276.
- Grahn, Y., Caputo, M.V., 1992. Early silurian glaciations in Brazil. Palaeogeogr. Palaeoclimatol. Palaeoecol. 99, 9–15.
- Grahn, Y., Melo, J.H.G., 1990. Bioestratigrafia dos quitinozoários do Grupo Trombetas nas faixas marginais da Bacia do Amazonas. PETROBRAS/CENPES/DIVEX/SEBIPE. Report produced for the Eletrobras Eletronort, Rio de Janeiro, p. 43.
- Grahn, Y., Paris, F., 1992. Age and correlation of the Trombetas group, Amazonas Basin, Brazil. Rev. Micropaleontol. 35, 197–209.
- Gray, J., 1840. Synopsis of the contents of the British Museum. In: London: British Museum, 42^o International Symposium Devonian System, vol. 2, pp. 921–935.
- Holmer, L.E., Popov, L.E., 2000. Lingulata. In: Williams, A., Brunton, C.H.C., Carlson, S.J. (Eds.), Treatise on Invertebrate Paleontology. Part H, Brachiopoda, Revised, vol. 2. Geological Society of America and University of Kansas Press, Boulder, pp. 30–146.
- Horodyski, R.S., Holz, M., Grahn, C.Y., Bosetti, E.P., 2014. Remarks on the sequence stratigraphy and taphonomy of the relictual Malvinokaffric fauna during the Kacák event in the Paraná Basin, Brazil. Int. J. Earth Sci. 103, 367–380.
- House, M.R., 1996. The middle Devonian Kacák event. In: Read at the Annual Conference of the Ussher Society, pp. 79–84.
- House, M.R., 2002. Strength, timing and cause of mid-Paleozoic extinctions. Paleogeograph. Palaeoclimatol. Paleoecon. 181, 5–25.
- Janvier, P., Melo, J.H.G., 1988. Acanthodian fish remains from the upper silurian or lower devonian of the Amazonas Basin, Brazil. Paleontology 31 (3), 771–777.
- Johnson, M.E., 2006. Relationship of Silurian sea-level fluctuations to oceanic episodes and events. GFF 128 (2), 115–121.
- Klemme, H.D., 1980. Petroleum basins – classification and characteristics. J. Pet. Geol., Beaconsfield 3 (2), 187–207.
- Kozłowski, R., 1913. Fósiles Dévoniens de l' état de Paraná (Brésil). Annales de Paléontologie Paris 8 (3), 1–19.
- Lange, F.W., 1943. Novos fósseis devonianos do Paraná. Arquivos Museu Paranaense 3, 223–225.
- Lange, F.W., 1954. Paleontologia Do Paraná: Volume Comemorativo Do 1^o Centenário Do Estado Do Paraná. Comissão de Comemorações do Centenário do Paraná, Curitiba, pp. 1–210.
- Lange, F.W., 1967. Subdivisão bioestratigráfica e revisão da coluna siluro-devoniana da bacia do baixo Amazonas. In: Simpósio sobre a biota amazônica. Belém. Atas, vol. 1, pp. 215–326.

- Lange, F.W., Petri, S., 1967. The devonian of the Paraná Basin. In: Bigarella, J.J. (Ed.), Problems in Brazilian Devonian Geology, vol. 21. Boletim Paranaense de Geociências, pp. 5–55, 22.
- Ludwig, G., 1964. Divisão estratigráfico-faciológica do Paleozoico da Bacia Amazônica. PETROBRAS, Ciência Técnica Petróleo, Seção: Exploração de petróleo 1, 1–72.
- Melo, J.H.G., 1985. A Província Malvinocáfrica No Devoniano Do Brasil: Estado Atual Dos Conhecimentos. Master's Dissertation. Geology Federal University of Rio de Janeiro, pp. 1–890.
- Melo, J.H.G., 1988. The malvinokaffric realm in the devonian of Brazil. In: Mcmillan, N. J., Embry, A.F., Glass, O.J. (Eds.), Devonian of the World, vol. 14. Canadian Society of Petroleum Geologists, Memoir, Calgary, pp. 667–703, 1.
- Méndez-Alzola, R., Sprechmann, P., 1971. Algunas orbiculoideas devónicas de la Precordillera de San Juan, rep. Argentina. Revista de la Asociacion Geologica Argentina 26 (4), 517–525.
- Mergl, M., 2001. Lingulate brachiopods of the silurian and devonian of the barrandian. Acta Musei Natl. Pragae, Ser. B - Hist. Nat. 57 (1–2), 1–49.
- Milani, E.J., França, A.B., Medeiros, R.A., 2007. Rochas geradoras e rochas reservatório da Bacia do Paraná, faixa oriental de afloramentos, Estado do Paraná. Bol. Geociencias Petrobras 15, 135–162.
- Northfleet, A.A., Medeiros, R.A., Mullmann, H., 1969. Reavaliação dos dados geológicos da Bacia do Paraná. Bol. Tec. Petrobras 12 (3), 291–346.
- Petri, S., 1948. Contribuição do estudo do Devoniano paranaense. Boletim da Divisão de Geologia e Mineralogia, DNPM 129, 1–125.
- Ponciano, L.C.M.O., Fonseca, V.M.M., Costa, M.D.M., 2012. Tafocenoses da Formação Pimenteira, Devoniano da Bacia do Parnaíba, Piauí: mapeamento, inventário e relevância patrimonial, vol. 35. Anuário do Instituto de Geociências, pp. 5–27, 1.
- Popov, L.E., Holmer, L.E., Bassett, M.G., Ghobadi, P.M., Percival, I.G., 2013. Biogeography of Ordovician linguliform and craniiform brachiopods. In: Harper, D. A.T., Servais, T. (Eds.), Early Palaeozoic Biogeography and Palaeogeography, vol. 38. Geological Society, London, Memoirs, pp. 117–126.
- Quadros, L.P., 1985. Distribuição bioestratigráfica dos Chitinozoa e Acritarchae na Bacia do Amazonas. Ph.D. Thesis, Universidade Federal do Rio de Janeiro.
- Reed, F.R.C., 1903. Brachiopoda from the Bokkeveld beds. South African Museum Annals 4, 165–197.
- Reed, F.R.C., 1925. Revision of the fauna of the Bokkeveld beds. South African Museum Annals 22, 27–225.
- Rocha, P.F., Silveira, R.R., Barbosa, R.C.M., 2019. Age and palaeoenvironments of the Manacapuru formation, presidente figueiredo (AM) region, lochkovian of the Amazonas Basin. Braz. J. Genet. 49 (4), 1–12.
- Sanford, R.M., Lange, F.W., 1960. Basin study approach to oil evaluation of Paranaíngosyncline, south Brazil. Am. Assoc. Pet. Geologists 44, 1316–1370.
- Schneider, R.L., Muhlmann, H., Tommasi, E., Medeiros, A., Daemon, R.F., Nogueira, A. A., 1974. Revisão estratigráfica da Bacia do Paraná. In: 28 °Congresso Brasileiro de Geologia, Porto Alegre. Anais 1, 41–65.
- Sharpe, D., 1856. Description of palaeozoic mollusca from South Africa. Trans. Geol. Soc. London 2 (7), 206–215.
- Souza, V.S., Nogueira, A.C.R., 2009. Manaus-Presidente Figueiredo (AM), borda norte da Bacia do Amazonas: um guia para excursão de campo. Rev. Bras. Geociencias 39 (1), 16–29.
- Steenmans, P., Rubinstein, C., Melo, J.H.G., 2008. Siluro-Devonian miospore biostratigraphy of the Urubu River area, western Amazonas Basin, northern Brazil. Geobios 41 (2), 263–282.
- Sudkamp, W.H., 1997. Discovered of soft parts of a fossil brachiopod in the “Hunsrückschiefer” (Lower Devonian, Germany). Paläontol. Z. 71, 91–95, 1997.
- Tomassi, H.Z., Almeida, C.M., Ferreira, B.C., Brito, M.B., Barberi, M., Rodrigues, G.C., Teixeira, S.P., Capuzzo, J.P., Gama-Júnior, J.M., Santos, M.G.K.G., 2015a. Preliminary results of paleontological salvage at Belo Monte Powerplant construction. Braz. J. Biol. 75 (3), 277–289.
- Tomassi, H.Z., Ferreira, B.C., Almeida, C.M., Barberi, M., Brito, M.B., Ramos, L.S., 2015b. Relatório Técnico Final do Programa de Salvamento do Patrimônio Paleontológico da Usina Hidrelétrica de Belo Monte. TERRAGRAPH Paleontologia. Belém 1, 1–50.
- Torsvik, T.H., Cocks, L.R.M., 2013. Gondwana from top to base in space and time. Gondwana Res. 24, 999–1030.
- Waagen, W., 1885. Productus limestone fossils. Palaeontology Indica 13 (1), 729–770.
- Wanderley Fiho, J.R., Melo, J.H.G., Fonseca, V.M.M., Machado, D.M.C., 2005. Bacias sedimentares brasileiras: bacia do Amazonas. Phoenix. Aracajú 7 (82), 1–6.
- Winrow, P., Sutton, M.D., 2014. Lingulate brachiopods and the early palaeozoic history of the iapetus ocean. Lethaia 47, 456–468.
- Zabini, C., Corniskey, J.C., Bosetti, E.P., 2013. John Mason Clarke e os lingulídeos e discinídeos dos estratos devonianos da Bacia do Paraná, estado do Paraná, Brasil: estado da arte. Revista Terr@ Plural 7, 43–58.
- Zabini, C., Furtado-Carvalho, A.B., Carmo, D., Assine, M.L., 2019. A new discinoid *Kosoidea australis* sp. nov. From the Iapó and Vila Maria formations, NE Paraná Basin, Brazil. Hist. Biol. 1–9.
- Zalán, P.V., Wolff, S., Conceição, J.C.J., Vieira, I.S., Astolfi, M.A.M., Appi, V.T., Zanotto, O.A., 1987. A divisão tripartite do Siluriano da Bacia do Paraná. Rev. Bras. Geociencias 17, 242–252.
- Zhang, Y., Lee, S., Wu, H.T., He, W.H., 2018. Palaeobiogeographical distribution of Orbiculoidea (Brachiopoda, Discinoidea) responding to global climatic and geographical changes during the Palaeozoic. Palaeontology 61 (2), 221–234.